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ORIGINAL PAPER

Vegetation structural characteristics and topographic factors in the remnant moist Afromontane forest of Wondo Genet, south central Ethiopia

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Abstract: For forest ecosystem management to be effective, knowledge of the horizontal and vertical structural diversity of a forest is essential. The moist Afromontane highlands of Wondo Genet in south-central Ethiopia present an opportunity to restore and rehabilitate and enhance the ecosystem services to be obtained from this forest sustainably. We focused on the forest structural characteristics to better understand the current forest conditions to assist in the sustainable management of this resource. A total of 75 (20 m × 20 m) quadrats were sampled and diameter at breast height (DBH) ≥2 cm and stem height ≥2 m were measured. Species identity and abundance, elevation, slope, and aspect were recorded for each plot. Structural characteristics were computed for each plot. Relationship of topographic factors with vegetation characteristics was conducted using R-Software. A total of 72 woody species was recorded. Whereas, the overall diameter distribution shows an inverted J-shaped curve, the basal area followed a bell-shaped pattern. Five types of population structures are revealed. The mean tree density and basal area was 397.3 stems·ha^{-1} and 31.4 m^2·ha^{-1}, respectively. Only 2.8% of the tree species have densities of >25 stems·ha^{-1} and the percentage distribution of trees show 56.2% in the DBH class 2–10 cm, indicating that the forest is dominated by medium-sized trees. *Celtis africana* (8.81 m^2·ha^{-1}) and *Pouteria adolfi-friedericii* (5.13 m^2·ha^{-1}) make the highest contribution to the basal area and species importance value index. The families/species with the highest importance value index are Ulmaceae, Fabacea and Sapotaceae. Species abundance (r^2 = 0.32, p <0.001) and species richness (r^2 =0.50, p <0.001) are positively related with tree density. Tree density is negatively related with elevation (r^2 = -0.36, p <0.001), slope (r^2 =-0.15, p <0.001) and aspect (r^2 = -0.07, p <0.05). While basal area is negatively related with elevation (r^2 =-0.14, p <0.001), it has a positive relationship with tree density (r^2 =0.28, p <0.001 and species richness (r^2 =0.098). Species with poor population structure should be assisted by restoration tasks and further anthropogenic disturbance such as illegal logging and fuel wood extraction should be restricted.

Keywords: forest structure; basal area; stratification; topographic factors; Afromontane forest

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Introduction

For effective forest ecosystem management, knowledge of forest conditions including their horizontal and vertical structural diversity is essential (Philip 1994; Liang et al. 2007). Limited knowledge of forest structural characteristics and factors governing structural diversity is often considered as the major constraining factor for their management, especially in sub-Saharan Africa (Godoy 1992). Several studies attempt to address vegetation structural diversity in relation to environmental gradients (e.g., Smith and Huston 1989; Huston (1979, 1994); Bale et al. 1998; Senbeta 2006; Yimer et al. 2006; Fontaine et al. 2007; Woldemariam Gole et al. 2008; Sharman et al. 2009). For example, the review of Huston (1979, 1994) show that patterns of species richness is determined by the interaction with environmental gradients and competitive exclusion.

Several studies also showed strong relationships between floristic composition and diversity to environmental gradients such as elevation, slope, and aspect (e.g. Smith and Huston 1989; Bale et al. 1998; Senbeta 2006; Yimer et al. 2006; Fontaine et al. 2007; Woldemariam Gole et al. 2008; Sharman et al. 2009). These gradients are determinants for the spatial and temporal distribu-

tion of factors such as radiation, precipitation, temperature, and soil conditions. They directly influence the pattern of diversity of plant species (Yimer et al. 2006; Albert and Christian 2007).

In a study of the Yayu forest in south-western Ethiopia, plant species distribution, and hence the patterns in forest vegetation, were found to be mainly influenced by the gradient in terrain variables such as altitude, slope, and distance from the river banks (Woldemariam Gole et al. 2008). Geographic and climatic conditions change sharply with altitude (Kharkwal et al. 2005) and vegetation in mountain regions responds to small-scale altitude variation (Bale et al. 1998). Similarly, Ovales and Collins (1986) evaluated soil variability across landscapes in two contrasting climatic environment and concluded that topographic position and variation in soil properties were significantly related. Slope also influences drainage, impacting soil formation processes, and chemical properties, consequently affecting floristic composition and structure (Woldemariam Gole 2008).

However, the nature of relationship between these environmental variables (altitude and slope) and species richness is variable due to its compound character; potentially encompassing external variables such as solar radiation budget (Holland and Steyne 1975) and cloud cover. The primary impacts of aspects are expressed through regulating energy budgets and site moisture relationships. Aspect-induced regimes of fundamental niche characteristics such as frost, light compensation level, and permanent wilting point enforces some sorting of species (Austin et al. 1990). The magnitudes of inter-aspect differences in mean monthly temperatures were sufficient to contribute to a sorting of canopy species (Bale et al. 1998). Local biotic interactions, such as competition and predation, and regional or historical processes, such as dispersal and speciation, might compound effects of topographic factors in affecting species richness (Cornell & Lawton 1992).

Here we present a study on vegetation structural characteristics in relation to environmental factors—mainly elevation, slope, and aspect. We assumed that these environmental conditions act as a filter and affect not only species composition but also vegetation structural diversity.

Materials and methods

Study site

Wondo Genet is situated in the south-eastern central highlands of Ethiopia, 263 km from Addis Ababa, at 7°5′30″ N to 7°7′40″ N latitude and 38°36′55″ E to 38°39′00″ E longitude on the eastern slope of the Rift Valley escarpment (Fig. 1). The large-scale physiographic setting is defined by a tectonic depression bounded by steep escarpments. The floor of the depression is covered by lakes, wetlands, and alluvial plains, which together cover half the watershed. The remaining half consists of uplands and escarpments with slopes varying between 8 and 85 degrees. The altitude ranges from 1800 m to 2500 m. The mean annual rainfall is about 1200 mm and is bimodal. Rain can be expected from March to April and June to August. November to February is relatively dry. The mean monthly temperature ranges from 19ºC in August to 25ºC in March, April, May, and September. The soils are young and of volcanic origin, characterized by well-drained loam or sandy loam, and are shallow on steep convex slopes but deeper at lower altitudes. The valley floor is partly covered by lake deposits well supplied with plant nutrients. On higher ground, the texture is sandy or silty, while clay dominates around the wetlands.

This forest is severely threatened by heavy anthropogenic disturbance and has declined from a 16% catchment land base to 2.8% within the past three decades alone, mainly driven by the expansion of small-scale agriculture, commercial farms, and logging. Current land use is predominantly small-holder agriculture with an average landholding size of less than one hectare per household. The major crops include Enset, Khat, sugarcane, maize, and potatoes. Wondo Genet is agriculturally fertile, with irrigation farming dominating in the flat and undulating sites. The Wondo Genet forest is the fragmented remnant of a formerly larger and more coherent forest covering the eastern rift flank (Dessie 2007). It harbors important and rare fauna and flora, and provides watershed, ecosystem, economic, research, and educational services. The population of the Wondo Genet is composed of six main ethnic groups together numbering about half a million (Dessie 2007).

Vegetation sampling

All woody plants (trees and shrubs) (≥2 cm diameter and ≥2 m height) were measured for diameter at breast height (DBH) and height, in 75 quadrats (20 m × 20 m). The first quadrat was located randomly, with subsequent quadrats established at 100 m an interval along a series of transects. The distance between transects was 350 m. Diameter was determined by caliper. Trees too large for the calipers were measured with a diameter tape. The measurements between the caliper and the diameter tape were calibrated. Tree height was measured using a Suunto Clinometer.

Plant identification was performed in the National Herbarium, Addis Ababa University. Nomenclature followed the published guidelines of the flora of Ethiopia and Eritrea (Hedberg and Edwards 1995; Edwards et al. 1995; Edwards et al. 1997; Edwards et al. 2000; Hedberg et al. 2003). Environmental parameters including slope (%) (Clinometer), elevation (m) (Garmin GPS-72, cross checked with altimeter), aspect (exposition) (using Silva compass), and coordinates (using GPS-72) were measured at each plot.

Data analysis

Data were analyzed using variant of analytical methods. "Tree Diversity Analysis" R-Software (Kindt and Coe 2005) was used to check for relationship of environmental gradient with structural characteristics. Pearson's critical value was used to check for significance level (at alpha =0.05). Aspect (exposition) was measured in degrees and converted to a scale of zero to one, following the formula: (1-cos (Ø- 45)/2, where Ø is aspect in

degrees, east of true north (McCune and Grace 2002) with zero being the coolest slope (northwest) and one being the warmest slope (southeast).

Horizontal structural characteristics such as the proportion of quadrats in which a species occurs in the total 75 sampled plots, abundance (the number of individual species per quadrat) and basal area were computed. The importance value index from Kent and Cooker (1992) was used to describe and compare the species' importance in the forest. The amount of "importance" is achieved by summing up values of relative density, frequency, and dominance.

The vertical stratification of trees was based on the method laid out in Lamprecht (1989) that divides the forest into layers (story or stratum). The ratio of abundance to frequency (A/F) was used to interpret distribution patterns of the species (Whitford 1949). If the A/F ratio is <0.025, the distribution is considered regular; if between 0.025−0.05, it is random; and if the ratio is >0.05, it is contagious (Curtis and Cottam 1956).

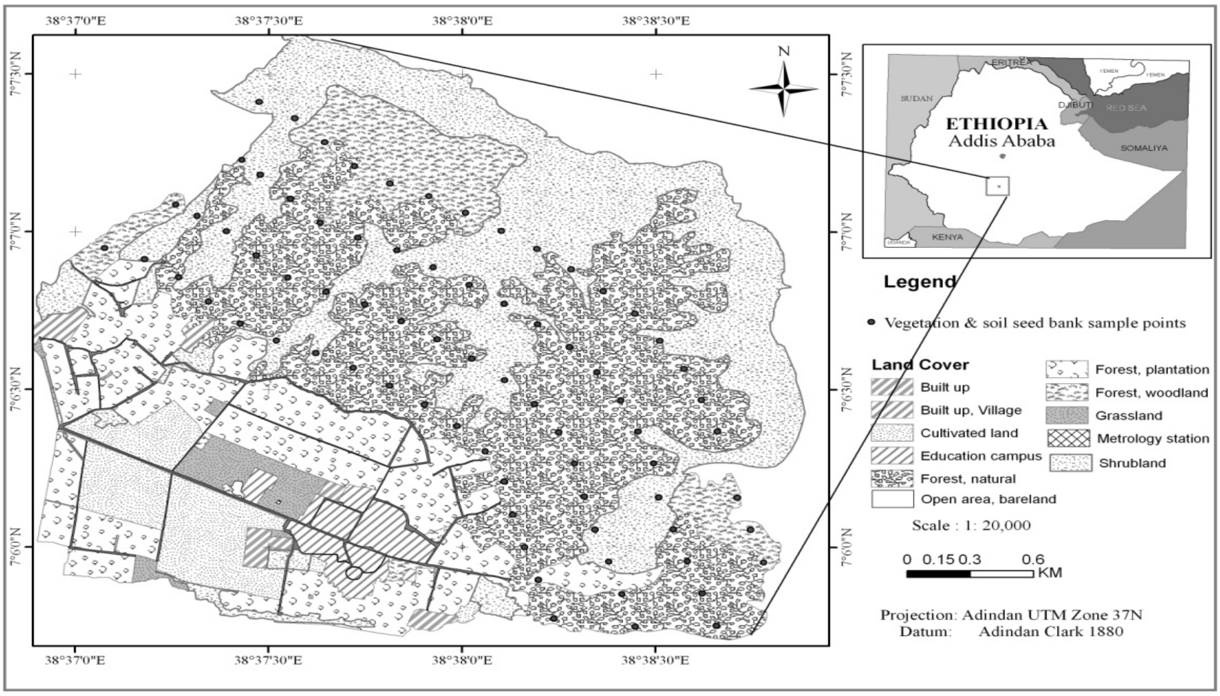

Fig. 1 Location map of study site and sample plots

Results

Effects of environmental gradients on species richness, density, and frequency distribution of woody plants

The overall Shannon-Wiener diversity and the evenness of the woody species in the forest were 3.63±0.438 and 0.84±0.10, respectively. The woody species richness of the forest was 72 species belonging to 41 families. The mean tree density (with diameter ≥2 cm, height ≥2 m) was calculated and resulted in 379.3 individuals per hectare. *Celtis africana* contributed 11.4% of the stem density followed by *Acokanthera schimperi* (10.2%), *Combretum molle* (6.1%), *Olea capensis* (5.8%), *Millettia ferruginea* (5.5%), *Cassipourea malosana* (5.0%) *and Vepris dainellii* (5.1%). Considering individuals with DBH ≥10 cm, only 45 species contributed to the total density of 166 individuals·ha^{-1}. In this group, Celtis *africana* contributed 21.3% of the density, followed by *Millettia ferruginea* (8.8%), *Combretum molle* (7.4%), *Acokanthera schimperi* (7%), *Vepris dainellii* (6.2%), and *Croton macrostachyus* (6%). With DBH >20 cm, only 38 (52% of the total) species contributed to the density (67.7 individuals·ha^{-1}). In this group, *Celtis africana* contributed (34.5%), followed by *Millettia ferruginea* (9.4%), *Croton macrostachyus* (8.9%), *Albizia schimperiana* (5.9%), and *Pouteria adolfi-friedericii* (4.9%).

Tree species were classified into six frequency classes and expressed in percentages. The majority (75%) of the tree species had a very low density of <5 stems·ha^{-1} (Fig. 2). Only 2.8% of the tree species had densities of >25 stems·ha^{-1}. Very few species are represented in class four (10 species, 14%), class five (3 species, 4%) and class six (2 species, 3%). The remaining species were distributed in class 3, class 2 and class 1 in increasing order, containing 14%, 19%, 24% respectively. Thus the trend shows that the higher the frequency class, the smaller the number of species found in the study plots. Consequently, this forest's frequency class distribution reveals the existence of a high degree of species turnover. The ratio of abundance to frequency that is used to interpret the distribution pattern of the species (regular, random, contagious) was calculated and resulted in a value >0.05 indicating a contagious distribution pattern.

Frequency is the proportion of quadrats in which a species occurs. It is a measure of occurrence of a given species in a given area. It is expressed as the number of quadrats in which a species was recorded per the total number of quadrats and expressed as a percentage. In this study, the majority of species had less than ten individuals per hectare (Fig. 3). Class 1 and class 2 contributed 43% of the species. Higher classes (class five and class six) contributed about 5% of the total species.

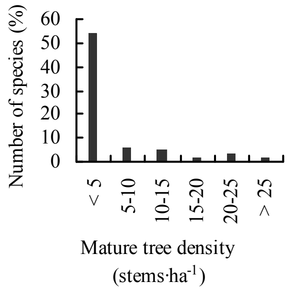

Fig. 2 Tree density for DBH >2 cm

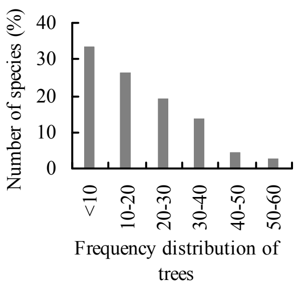

Fig. 3 Frequency distribution of trees

The relationship of tree density with species abundance and species richness was determined. Significantly positive relationship of tree density with species abundance (r^2 = 0.32, p <0.001) (Fig. 4 a) and species richness (r^2 = 0.50, p <0.001) (Fig. 4 b) was observed. Analysis of the relationship of elevation, slope, and aspect with tree density was conducted and showed a significant but negative relationship. Elevation (r^2 = -0.36, p <0.001) was significantly and negatively correlated with tree density (Fig. 5a). Similarly, tree density showed significantly negative relationship with slope (r^2 = -0.15, p <0.001) (Fig. 5b) and aspect (r^2 = -0.068, p <0.05), (Fig. 5 c).

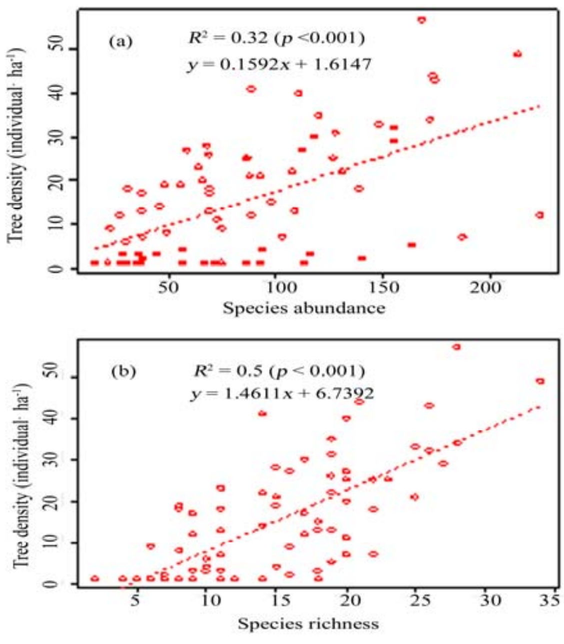

Fig. 4 Relationship of species abundance and species richness with tree density

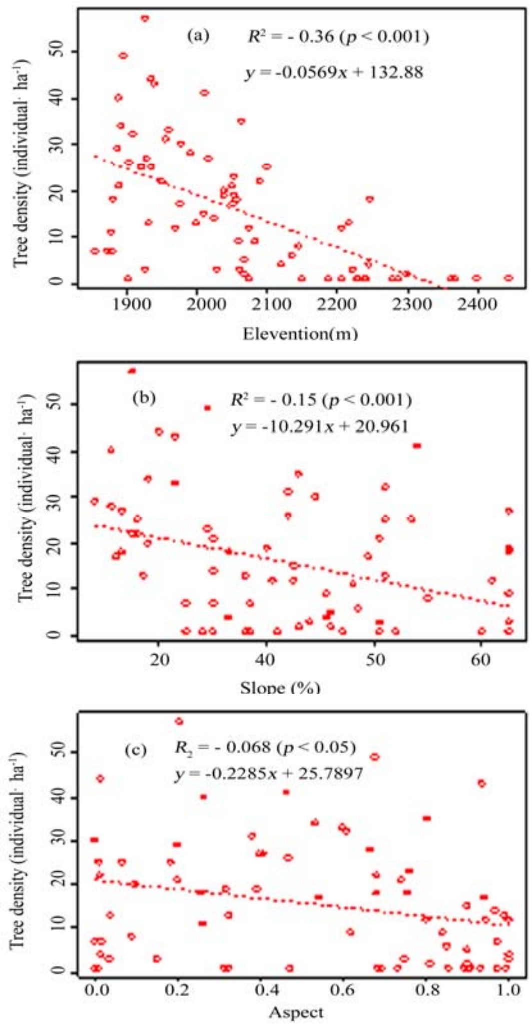

Fig. 5 Relationship of tree density with elevation, Slope and aspect

The diameter class distribution showed an inverted-J shaped curve with a sharp drop in the higher diameter classes (Fig. 6). There is a break in the curve at the 8th diameter class. The sharp decline and very low representation in the higher diameter class indicate the selective logging of the forest's most valuable trees. The size distribution showed 56.2% in the DBH class 2–10 cm followed by 26.2% in class11–20 cm, 8.3% in class 20–30 cm, 5.0% in class 30–40 cm, 2.3% in class 40–50 cm, 1.05% in class 50–60 cm, 0.4% in the class 60–70 cm, 0.2% in the class 70–80 cm and 0.4% DBH >80 cm. This indicates that most trees are in the lower diameter classes (<20 cm). The presence of some large trees and the prevalence of small- to medium-sized individuals may indicate that the forest is in a secondary development stage. The dominant large diameter forest trees with a DBH >81 cm were *Pouteria adolfi-friedericii*, Celtis *africana*, *Croton macrostachyus*, *Ficus vasta*, *Olea welwitschii*, *Podocarpus falcatus*, *Syzygium guineense*, *Vepris dainellii*, and *Polyscias fulva.*

The overall basal area was 31.4 m^2·ha^{-1}. Unlike the pattern of diameter distribution (inverted-J shaped curve), the basal area distribution showed a bell-shaped curve with the peak near the middle (diameter class 4, 30–40 cm) characterizing the forest as a young secondary forest (Fig. 7a). About 28% of the total basal

area is *Celtis africana*, followed by *Pouteria adolfi-friedericii* (16.3%) and *Acokanthera schimperi* (3.9%). About 60.8% of the total basal area included five tree species: *Celtis africana*, *Pouteria adolfi-friedericii*, *Acokanthera schimperi*, *Albizia schimperiana*, and *Millettia ferruginea*. Most of other species contributed less than 1m^2·ha^{-1} (Fig. 7b).

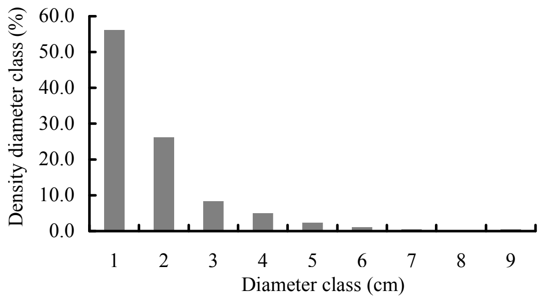

Fig. 6 Frequency distribution of trees in DBH classes in the forest. Figs based on relative DBH (%); Class 1 is 2-10 cm; Class 2 is 10–20 cm; Class 3 is 20–30 cm; Class 4 is 30–40 cm; Class 5 is 40–50 cm; Class 6 is 50–60; Class 7 is 60–70; Class 8 is 70–80; Class 9 is >80 cm.

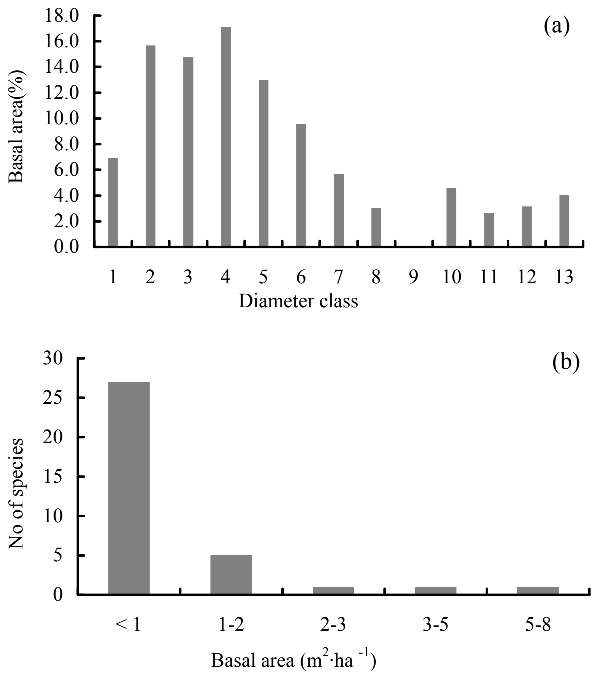

Fig. 7 Basal area versus diameter class distribution. Class 1 is 2-10 cm; Class 2 is 10–20 cm; Class 3 is 20–30 cm; Class 4 is 30–40 cm; Class 5 is 40–50 cm; Class 6 is 50–60 cm; Class 7 is 60–70 cm; Class 8 is 70–80; Class 9 is 80–90 cm; Class 10 is 90–100 cm; Class 11 is 100–110 cm; Class 12 is 110–120 cm; Class 13 is 120–130 cm, and the proportion of the species contributing to the basal area.

The relationship of environmental gradients and vegetative density with basal area was computed. Basal area was positively and significantly related with tree density (r^2 = 0.285, p <0.001), and species richness (r^2 =0.098, p <0.01) (Fig. 8 a, b). Elevation was significantly and negatively related with basal area (r^2 = -0.14, p <0.001) (Fig. 8 c). However, the relationship of both slope and aspect with basal area was not significant.

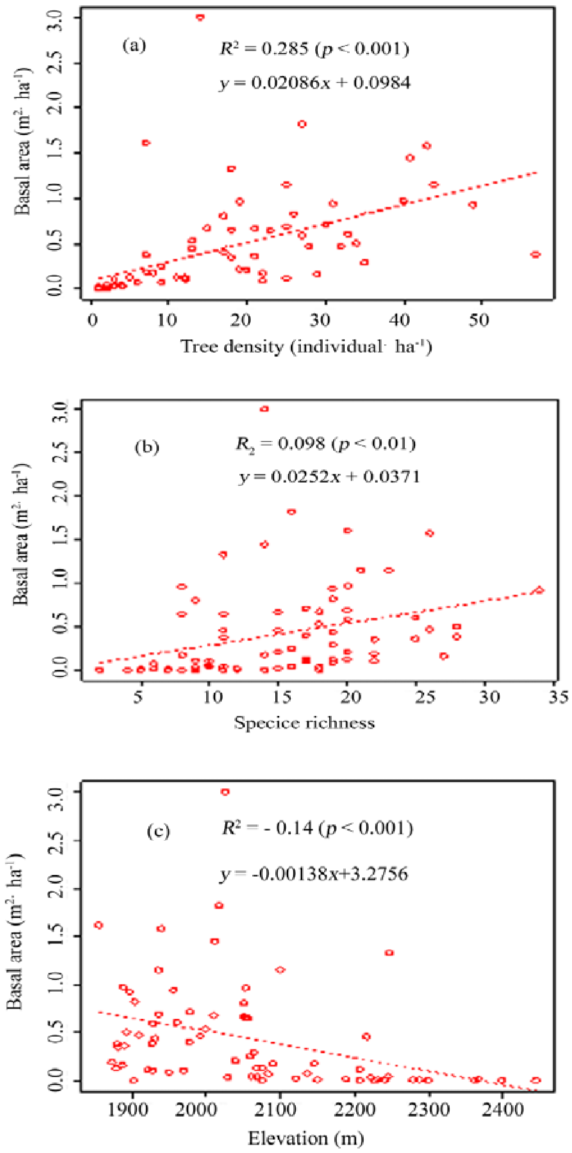

Fig. 8 Relationship of elevation, tree desnity and species richness with basal area

Species importance value index (SIV)

The importance value index (IVI) developed by Curtis and McIntosh (1951) was used to correlate individual analysis and findings in vegetation structure. This is calculated for each species by adding relative abundance (RA) with relative frequency (RF) and relative dominance (RDo). Table 1 shows the species with the highest SIV. The three species with the highest SIV are as follows: *Celtis africana* 8.81 m^2·ha^{-1} (28% of the total basal area, 11.42% of the stem density), *Pouteria adolfi-friedericii* 5.13 m^2·ha^{-1} (16.32 of the total basal area and 2.11% of the total density), and *Acokanthera schimperi* 1.22 m^2·ha^{-1} (3.88 of the total density and 10.21% of the total stem density).

Table 1. Species importance value index in Wondo Genet natural forest

Species	F*	RF	D	RD	Basal area ($m^2 \cdot ha^{-1}$)	RDO	IVI
Celtis africana Burm.f.	56.0	4.1	43.3	11.4	8.8	28.0	43.5
Pouteria adolfi-friedericii (Engl.) Baehni	21.3	1.6	8.0	2.1	5.1	16.3	20.0
Acokanthera schimperi Oliv.	30.7	2.2	38.7	10.2	1.2	3.9	16.3
Albizia schimperiana Oliv.	40.0	2.9	9.3	2.5	2.2	7.1	12.5
Millettia ferruginea Hochst.	20.0	1.5	21.0	5.5	1.7	5.5	12.5
Combretum molle R.Br. ex.G.Don	26.7	1.9	23.0	6.1	1.1	3.4	11.4
Croton macrostachyus Hochst. ex Delile.	33.3	2.4	11.0	2.9	1.8	5.6	10.9
Afrocarpus falcatus (Thunb.) Mirb	32.0	2.3	11.0	2.9	1.7	5.4	10.7
Cassipourea malosana Alston	42.7	3.1	19.0	5.0	0.7	2.3	10.4
Olea capensissubsp Welwitschii (Knobl.) Gilg & Schellenb.	32.0	2.3	22.0	5.8	0.6	1.8	10.0
Vepris dainellii (Pic. Serm.) Kokwaro	28.0	2.0	19.0	5.0	0.8	2.6	9.6
Maytenus arbutifolia (Hochst. ex A.Rich) R. Wilczek	56.0	4.1	13.3	3.5	0.2	0.5	8.1
Teclea nobilis Delile	38.7	2.8	14.0	3.7	0.2	0.6	7.1
Syzygium guineense DC. *subsp guineense*	24.0	1.7	11.0	2.9	0.3	0.8	5.5
Calpurnia aurea Benth.	41.3	3.0	5.0	1.3	0.0	0.1	4.5
Buddleja polystachya Fresen.	40.0	2.9	4.3	1.1	0.1	0.3	4.4
Fagaropsis angolensis Engl.) H.M.Gardner	21.3	1.6	4.0	1.1	0.4	1.3	4.0
Chionanthus mildbraedii (Gilg & G. Schellenb.) Stearn	21.3	1.6	5.3	1.4	0.3	0.9	3.8
Canthium oligocarpum Hiern	26.7	1.9	3.7	1.0	0.1	0.5	3.4
Rhus vulgaris Meikle	40.0	2.9	1.3	0.4	0.0	0.1	3.3
Myrsine africana L.	44.0	3.2	0.3	0.1	0.0	0.0	3.3
Bersama abyssinica Fresen	28.0	2.0	4.3	1.1	0.0	0.0	3.2
Erythrococca trichogyne Prain.	30.7	2.2	3.3	0.9	0.0	0.1	3.2
Diospyros mespiliformis Hochst. *ex A.DC*	40.0	2.9	0.7	0.2	0.0	0.0	3.1
Nuxia congesta R. Br.	17.3	1.3	5.0	1.3	0.2	0.5	3.1
Polyscias fulva (Hiern) Harms	10.7	0.8	4.3	1.1	0.4	1.2	3.1
Osyris quadripartita Salzam. ex Decne.	26.7	1.9	3.0	0.8	0.1	0.3	3.0
Allophylus macrobotrys Gilg	26.7	1.9	3.7	1.0	0.0	0.0	3.0
Pittosporum viridiflorum Sims	21.3	1.6	3.7	1.0	0.1	0.3	2.8
Lepidotrichilia volkensii (Güerke) J. –F.Leroy	9.3	0.7	5.0	1.3	0.3	0.8	2.8
Diospyros abyssinica subsp abyssinica (Hiern) F. White	14.7	1.1	2.3	0.6	0.3	0.9	2.6
Dodonaea angustifolia L. f.	24.0	1.7	3.0	0.8	0.0	0.0	2.6
Cordia africana Lam.	6.7	0.5	3.7	1.0	0.4	1.1	2.6
Draceana steudneri Engl.	16.0	1.2	1.7	0.4	0.3	0.9	2.5
Flacourtia indica (Burm.f) Merr.	18.7	1.4	2.7	0.7	0.1	0.4	2.5
Schrebera alata Welw.	20.0	1.5	2.7	0.7	0.0	0.2	2.3
Coffea arabica L.	26.7	1.9	1.3	0.4	0.0	0.0	2.3
Protea gaguedi J.F. Geml.	21.3	1.6	2.0	0.5	0.1	0.2	2.3
Oxyanthus speciosus DC.	13.3	1.0	4.0	1.1	0.0	0.1	2.2
Ficus sur Forssk.	5.3	0.4	1.3	0.4	0.4	1.4	2.1
Psydrax schimperiana (A. Rich.)	14.7	1.1	3.7	1.0	0.0	0.1	2.1
Rhus retinorrhoea Steud. ex Oliv.	18.7	1.4	1.7	0.4	0.0	0.1	1.9
Allophylus abyssinicus Radlk	5.3	0.4	1.3	0.4	0.3	1.0	1.7
Vernonia auriculifera Hiern	17.3	1.3	1.3	0.4	0.0	0.0	1.7
Maesa lanceolata Forssk.	17.3	1.3	1.0	0.3	0.0	0.1	1.6
Erica arborea L.	14.7	1.1	2.0	0.5	0.0	0.0	1.6
Abutilon bidentatum (Hochst.) ex A. Rich.	12.0	0.9	2.3	0.6	0.0	0.1	1.6
Premna Schimperi Engl.	17.3	1.3	1.0	0.3	0.0	0.0	1.6
Olinia rochetiana A. Juss.	9.3	0.7	2.3	0.6	0.1	0.2	1.5
Carissa spinarum L.	9.3	0.7	2.7	0.7	0.0	0.0	1.4
Ekebergia capensis Sparrm.	9.3	0.7	1.3	0.4	0.1	0.3	1.4
Hypericum revolutum Vahl	17.3	1.3	0.3	0.1	0.0	0.0	1.4
Clerodendrum myricoides R.Br.	17.3	1.3	0.3	0.1	0.0	0.0	1.4
Prunus africana (Hook.f.) Kalkman	4.0	0.3	0.7	0.2	0.3	0.8	1.3
Vernonia hochstetteri Sch.Bip. ex Hochst.	10.7	0.8	1.7	0.4	0.0	0.1	1.3
Olea europaea L. *subsp cuspidata*	16.0	1.2	0.3	0.1	0.0	0.0	1.3
Dracaena afromontana Mildbr.	9.3	0.7	1.3	0.4	0.0	0.1	1.1
Oncoba spinosa Forssk.	5.3	0.4	2.0	0.5	0.0	0.2	1.1

Continued Table 1

Species	F*	RF	D	RD	Basal area ($m^2 \cdot ha^{-1}$)	RDO	IVI
Hypericum quartinianum A.Rich.	9.3	0.7	0.7	0.2	0.0	0.0	0.9
Grewia ferruginea Hochst.	9.3	0.7	0.3	0.1	0.0	0.0	0.8
Ficus thonningii Blume.	2.7	0.2	0.3	0.1	0.1	0.4	0.7
Ehretia cymosa Thonn.	2.7	0.2	1.3	0.4	0.0	0.1	0.6
Ficus vasta Forssk.	1.3	0.1	0.3	0.1	0.1	0.4	0.6
Phoenix reclinata Jacq.	6.7	0.5	0.3	0.1	0.0	0.0	0.6
Clutia lanceolata Forssk.	6.7	0.5	0.3	0.1	0.0	0.0	0.6
Steganotaenia araliacea Hochst.	2.7	0.2	0.7	0.2	0.0	0.0	0.4
Apodytes dimidiata E. Mey. ex Arn.	4.0	0.3	0.3	0.1	0.0	0.0	0.4
Acacia abyssinica Hochst. ex Benth	2.7	0.2	0.7	0.2	0.0	0.0	0.4
Acanthus eminens C. B. Clarke	2.7	0.2	0.3	0.1	0.0	0.0	0.3
Entada abyssinica Steud.	1.3	0.1	0.3	0.1	0.0	0.0	0.2
Maytenus undata (Thunb.) Blakelock	1.3	0.1	0.3	0.1	0.0	0.0	0.2
Syzygium guineense DC. Subsp. *macrocarpum*	1.3	0.1	0.3	0.1	0.0	0.0	0.2

Notes: * F is Frequency, RF is Relative frequency, D is density, RD is Relative density, RDO is Relative dominance, IVI is Species importance value index.

Family importance value index (FIV)

The family importance value index was computed from relative density, relative diversity and relative dominance as given by Curtis and McIntosh (1951). The result showed the family with the highest FIV was Ulmaceae with a basal area of 8.81$m^2 \cdot ha^{-1}$ (28% of the basal area, 11.3% stem density) followed by Fabaceae, basal area of 4.03 $m^2 \cdot ha^{-1}$ (12.8% of the basal area, 9.5% of stem density), and Sapotaceae, with a basal area of 5.42 $m^2 \cdot ha^{-1}$ (17.2% of the total basal area, 2.7% of the stem density). The most dominant families and species are also those which have the highest SIV (Curtis and McIntosh 1951). This is in agreement with the present study as the dominant families include Ulmaceae (FIV =43.5), Fabaceae (FIV=30.1) Sapotaceae (FIV =22.6), and Rutaceae (FIV=20.7). These four families are distinctly dominant in term of FIV and together contribute more than 62.6% of the total basal area. The top ten FVI contributed 86.3% of the total basal area, 70.18% of the total density.

Species population structure

Tree species population structures were separated into five main population distributions (Fig. 9 a-e). These include: a) Species with a fairly even frequency distribution in all DBH classes (e.g., *Diospyros abyssinica*); b) A Gauss-type or bell-shaped distribution pattern, with the first and second class DBH classes having a low frequency, a gradual increase in the number of individuals in the medium classes and then a subsequent decrease in frequency toward the higher DBH classes (e.g., *Cordia africana,* and *Croton macrostachyus*). Species with this type of distribution typically have fewer stems in the smaller diameter classes and more in the intermediate classes. c) Reverse J-shape curve that indicates a pattern where the highest frequency is in the lower diameter classes and gradual decrease towards the higher classes (e.g., *Albizia schimperiana,* and *Cassipourea malosan*). These are called stable or expanding species due to their continuous recruitment and expanding population. d) Broken reverse J-shape (e.g., *Pouteria adolfi-friedericii,* and *Afrocarpus falcatus,* and *Lepidotrichilia volkensii*), where the highest frequency is in the lower diameter classes but interrupted at one or more points in the middle classes. Selective logging might have taken out the diameter that could be logged out, leaving the very young and the very old ones on the site. e) A pattern where both the small diameter and close to highest diameter class is broken (e.g., *Allophylus abyssinicus*, *Polyscias fulva*, *Millettia ferruginea*, and *Syzygium guineense*).

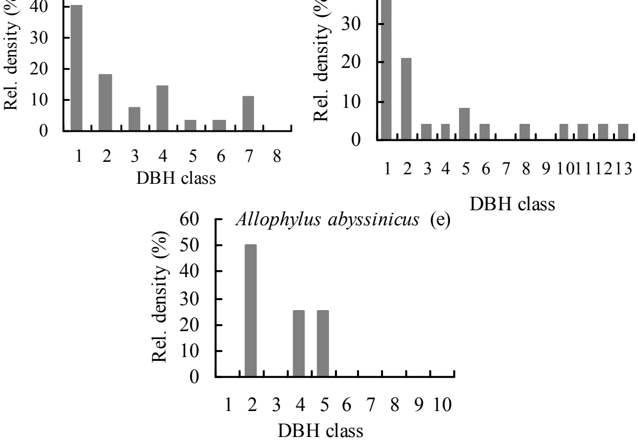

Fig. 9 Representative patterns of frequency distribution of trees tree density values over DBH classes (cm). Class 1 is 2–10 cm; Class 2 is 10–20 cm; Class 3 is 20–30 cm; Class 4 is 30–40 cm; Class 5 is 40–50 cm; Class 6 is 50–60 cm; Class 7 is 60–70 cm; Class 8 is 70–80 cm; Class 9 is 80–90 cm; Class 10 is 90–100 cm; Class 11 is 100–110 cm; Class 12 is 110–120 cm; Class 13 is 120–130 cm.

Tree height and vertical stratification

Fig. 10 shows how tree density decreases sharply as the height class increases. Using the IUFRO classification scheme, the highest number of individuals were found in the lower height classes, 99 stems·ha^{-1} (26.1%), followed by the middle classes 93.3 stems·ha^{-1} (24.6%) and the upper classes, 60.3 stems·ha^{-1} (15.9%). With the tallest tree, *Pouteria adolfi-friderecii* measuring 42 m, the lower, middle and upper story will be 14, 14–28 and > 28 m, respectively. The result of dividing tree density into the three strata (lower, middle and upper story) places 74.4% of the trees into the lower story, 22.7% in the middle story and 2.6% in the upper story. Five of the most abundant lower-story tree species include: *Acokanthera schimperi* (12.7%), *Combretum molle* (7.5%), *Olea capensis* subsp *Welwitschii* (7.2), *Cassipourea malosana* (5.7%), *Vepris dainellii* (5.4%), and *Teclea nobilis* (4.9*)*. Interestingly, none of these species made any contribution to the highest height class. The middle story (14–28 m) is dominated by *Celtis africana* (34.9%), *Millettia ferruginea* (12.4%), *Croton macrostachyus* (7.8 %), *Albizia schimperiana* (5.0), *and Vepris dainellii* (3.8). The upper story (28–42 m) is dominated by only a few tree species, including: *Celtis africana* (26.7), *Pouteria adolfi-friedericii* (26.7%), *Croton macrostachyus* (13.3%), *Afrocarpus falcatus* (13.3%), and *Albizia schimperiana* (10%)

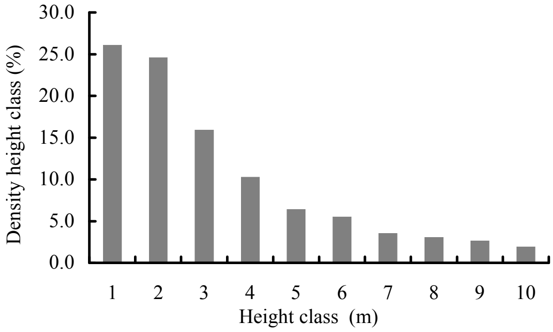

Fig. 10 Frequency distribution of tree density by height classes. Figs based on relative density (%); Class 1 is 2–6 m; Class 2 is 6–9 m; Class 3 is 9–12 m; Class 4 is 12–15 m; Class 5 is 15–18 m; Class 6 is 18–21 m; Class 7 is 21–24 m; Class 8 is 24–27 m; Class 9 is 27–30 m; Class 10 is >30 m.

The highest number of species (65) and stem density (74.7%) is found in the lower strata. The middle story yields 27% of the species and 22.7% of the stems. The upper story has very few stems (2.6%) and 8% of the species (Table 2).

Table 2. The basal area (m^2·ha^{-1}) and number of species along the height strata (stems·ha^{-1})

Storey	Number of stems	%	Number of species	%	Basal area	%	Ratio of individuals to species
Lower	283.33	74.7	69	65	6.96	22.1	4.1 :1
Middle	86.00	22.7	29	27	13.14	41.7	2.97 :1
Upper	10.00	2.6	8	8	11.43	36.2	1.25 :1

Discussion

Stem density distribution and relationships along environmental gradient

The results of our study on the relationship of elevation, slope, and aspect with tree density distribution fall in line with other authors. Ellu and Obusa (2005) reported that elevation and slope influences species richness and the dispersion behavior of tree species. In Yayu forest, in south-western Ethiopia, Woldemariam Gole et al. (2008) found that plant species distribution, and hence the patterns in forest vegetation were mainly influenced by the gradient in terrain variables such as altitude, slope and distance from the river banks. Sharman et al. (2009) determined that altitude was significantly and negatively correlated with density and species richness.

Our findings show that both tree density and basal area was negatively correlated with elevation. In the study area, the steeper slopes and higher elevation had sparse trees with shorter stature. These environmental gradients affected moisture regime that affected soil formation processes. The steeper slopes and higher elevation had a very shallow soil that invariably influenced recruitment and mortality and hence lower tree density.

Although not addressed here, wood extraction (firewood and timber) through illegal logging has thinned the stands in the lower, more easily accessible elevation and slopes. When compared to other similar Afromontane forests of Ethiopia, this forest fragment has very disturbed structural characteristics. With a mean tree density of 379 stems·ha^{-1}, the Wondo Genet forest is less than similar montane forests of Ethiopia. For example, Lulekal (2008) recorded a density of 408 stems·ha^{-1} at the Mena Angetu forest, in southeastern Ethiopia while Bekele (1994) recorded a density of 565 stems·ha^{-1} at the Jibat forest, 638 at Chilimo, 484 at Menagesha, and 329 at Wof-washa. Due to selective logging, Wondo Genet forest is dominated by small-sized trees. At Wondo Genet, trees with a DBH between 2 and 10 cm contributed 56% of stem density. In the present study, the woody species richness with DBH $\geq$2 cm was 72. The species richness declines to 45 species for DBH >20 cm and 28 species for DBH >20 cm. Species abundance also declined with an increase in diameter size.

Lulekal et al. (2008) recorded a similar pattern in Mena Angetu moist montane forest, southeastern Ethiopia, where woody species richness was 50 species for DBH >2 cm, 45 species for DBH > 10 cm and 35 species for DBH >20 cm. In the same study, abundance declined from 408 to 292 to 139 individual species·ha^{-1}, respectively. However, the difference between Mena Angetu moist montane forest and Wondo Genet moist montane forest for DBH> 2 cm is only 29 stems·ha^{-1} whereas the difference in density with DBH >10 cm is 126 stems·ha^{-1}. This suggests that that Wondo Genet forest was subjected to more selective logging of the larger diameter class.

Elsewhere in the tropics, reports of mean stand densities include: 709 stems·ha^{-1} in northern Andhra Pradesh (Sudhakar et al. 2011), Costa Rica, 448 to 617 stems·ha^{-1} (Heaney et al. 1990),

Brazil from 420 to 777 stems·ha^{-1} (Campbell et al. 1992), and Malaysia from 250 to 500 stems·ha^{-1}. By comparison, Wondo Genet is severely degraded, being far below these tropical forests density counts. The ratio of density of trees with DBH >10 cm to DBH >20 cm is taken as a measure of the distribution of the size classes (Grubb et al. 1963). Wondo Genet forest had a ratio of 2.45, indicating the predominance of small trees. Using this ratio, tree density in Wondo Genet can be compared with other Ethiopian montane forests. The forest ratio is close to Menagesha (2.3), Chilimo (2.6) (Bekele 1994) but far less than Jibat (2.0), Wofwasha (1.5) Bekele (1994), and Mena Angetu (2.09) (Lulekal et al. 2008). The Wondo Genet forest has a species rarity measure (those represented by $\leq$ 2 individuals·ha^{-1}) of 48.6%. Frequency gives an approximate indication of the homogeneity or heterogeneity of the stand under consideration (Kent and Coker 1992). In Wondo Genet, the frequency values display a high turnover or diversity of tree species. The species that belonged to the highest frequency classes (four and five) ranged from 4%–14%. Lamprecht (1989) found 5%–15% of species belonging to the highest frequency classes (four and five) which were regarded as integral components of the species mixture. In the present study, the ratio of species to individuals per hectare differed along the strata ranging from 1.29:1 to 1:4. In tropical moist montane forests and low-land rainforests, ratios up to 1:7 were recorded (Lamprecht 1989). The high dominance of a few species in the Afromontane rainforests could be attributed to a number of factors, such as the overharvesting of desired species, disturbance factors, the succession stage of the forest, species survival strategies, and dispersal mechanisms (Senbata 2006). Species that are able to survive and flourish after disturbance tends to be those that reproduce rapidly and abundantly (McKinney, 1997) and are dispersed widely. Gentry (1988) hypothesized that species dominance is never predictable in tropical forests and is most likely determined by stochastic processes.

Tree-density variation can be directly correlated to species abundance and richness (species diversity), and topographic factors (elevation, slope, and aspect). In the present study, diversity is positively and significantly related to stem density. Increased productivity resulting from increased species diversity decreases overall mortality during drought (Mulder et al. 2001). Stress-dependent facilitation benefits most young trees, reducing vulnerability to drought. Maintaining plant diversity is an important means to obtain a high growth rate (Liang et al. 2007). In the Wondo Genet study, tree density was negatively and significantly related with elevation, slope, and aspect. Sahu et al. (2008) reported that the number of species, stem density and α-diversity and its components declined as altitude increased.

Stem diameter distribution and population structure

One of the most important stand variables to consider in sustained-use management system development is stand and species diameter distribution (Geldenhuys and Murray 1992). The diameter–frequency distribution of individual species or group of species may offer a very different picture. A species' stem-diameter distribution varies greatly with plot size. Some species that have a bell-shaped distribution within a small plot could show a reverse J-shape when plot sizes are increased. Sufficiently large sample plots are necessary to ensure representative results (Lamprecht 1989). In the present study, the overall diameter-frequency distribution followed the inverted J-shaped curve with a sharp drop in the larger diameter frequency distribution as well as a breakage in the highest diameter class (Sokpon and Biaou 2002). Senbata (2006) stated that the forest's reproductive capacity must be sufficient to sustain the forest, and the population structure of most species must have inverted J-shaped distribution.

In Ethiopia, logging has been extremely selective and mainly confined to a few highly valuable timber tree species and broken frequency distributions are the result of such activities (Senbata 2006). In the present study, several species showed a deviation from the reverse J-shaped healthy population structure while other species showed a fairly even frequency distribution in all DBH classes.

The bell-shaped pattern of distribution maintained by some Wondo Genet species describes a situation of poor reproduction. This condition is likely due to the decline in the number of large trees. Though the inverse J- shape still describes some species, breakage in the curve was observed in the higher diameter classes due to selective logging. Breakage that occurred both in the lower and higher diameter classes indicates the risk to population reproduction. Species like *Pouteria adolfi-fiedericii* had a similar broken-inverted J-shaped structure in Bonga, Harena, Maji, Berhane Kontir and Yayu montane forests of Ethiopia (Senbeta 2006). This implicates nation-wide selective logging of several species for their valued timber.

The *Afrocarpus falcatus* population structure at Wondo Genet had a similar pattern as other central highlands montane forests (Bekele 1994). The pattern shows a high frequency at the lower DBH classes but becomes irregular toward higher classes indicating good reproduction but discontinuous recruitment. Teketay (1995) and Tesfaye et al. (2008) have reported similar results from the different Afromontane forests of Ethiopia.

The natural patterns in a population structure curve show the silvicultural characteristics of a species. The characteristic inverted J-shaped curve, or negative exponential stem distribution, shows the shade-tolerant species have an all-age population structure (Sokpon and Biaou 2002). These species are stable as far as equilibrium stand distribution is concerned (Veblen et al. 1980). In the present study, *Celtis africana* can be considered a stable species. The bell-shaped distribution species are generally light-demanding trees. They are gap dependent for their regeneration as early life stage mortality is higher under a closed forest canopy.

Basal-area distribution and important value index

The basal area distribution of a stand follows a bell-shaped curve with a peak or maximum which increases over time: e.g., 35 cm diameter class center for young secondary forest, 65 cm for old secondary forest. The Wondo Genet forest has its basal area peak at the 4th diameter class (30–40 cm) with the diameter class cen-

tered at 35 cm. This indicates that Wondo Genet forest has a young secondary forest.

Site productivity, competition, anthropogenic disturbance and density affect the basal area of the forest stands. In Ethiopia, anthropogenic disturbance have greatly affected the forests' basal area. Comparing the Wondo Genet forest with other montane forests of Ethiopia provides an insight about the status of this forest. With a basal area of 31.4 $m^2 \cdot ha^{-1}$, Wondo Genet was only higher than that of Chilimo (30 $m^2 \cdot ha^{-1}$) (Bekele 1994); but far less than Menagesha (36 $m^2 \cdot ha^{-1}$), (Bekele 1994); Dindin (49 $m^2 \cdot ha^{-1}$), (Shibru & Balcha 2004); Masha Anderacha (82 $m^2 \cdot ha^{-1}$) (Yeshitela & Bekele 2003), Denkoro (45 $m^2 \cdot ha^{-1}$) (Ayalew et al. 2006), Bonga (47$m^2 \cdot ha^{-1}$), Berhane Kontir (54 $m^2 \cdot ha^{-1}$), Harenna (49 $m^2 \cdot ha^{-1}$), Maji (53 $m^2 \cdot ha^{-1}$) and Yayu forests (46 $m^2 \cdot ha^{-1}$) (Senbata 2006). The lower basal area recorded in the present study is mainly due to illegal cutting.

In terms of individual species contribution, 60.8% of the total basal area involves five tree species: *Celtis africana*, *Pouteria adolfi-friedericii*, *Acokanthera schimperi*, *Albizia schimperiana*, and *Millettia ferruginea. Pouteria adolfi-friedericii* alone represented 16.3% of the basal area. These species contribute far more than just basal area. They greatly influence the ecosystem function of this remnant forest by providing a microclimate for the recruitment and survival of other forest species under their canopy. In this study, relationship between tree species richness and basal area was observed. Liang et al. (2007) reported that as tree species diversity increased, net basal growth increased both substantially and linearly.

Curtis and McIntosh (1951) have attempted to develop a method to correlate individual analysis findings known as the Importance Value Index (IVI). This index is computed for each species or family by adding relative abundance, relative frequency, and relative dominance, thus permitting a comparison of the ecological significance of a species or family in a given forest type. A high SIV/FVI index indicates that the species or family sociological structure in the community is high (Lamprecht 1989). Surveys that yield a similar importance value index for a characteristic species or family should indicate the same or at least similar stand composition and structure, site requirements, and comparable dynamics (Lamprecht 1989).

The leading dominant and ecologically most significant trees with high SIV index were *Celtis africana*, *Pouteria adolfi-friedericii* and *Acokanthera schimperi.* In terms of family, Ulmaceae, Fabaceae, and Sapotaceae contributed the highest FIV. The leading dominant and ecologically most significant species might also be the most successful species in regeneration, pathogen resistance, shade tolerance, and aggressive growth, while being the least preferred by browsing animals (Uriarte et al. 2005).

Vertical stratification

The differentiation into layers between ground level and the canopy constitutes the vertical structure of a forest (Bourgeron 1983). The degree of stratification within a community is related to the degree of "functional" stratification (or density) in the canopy (Liira et al. 2002) ; the character of physical environment (Kent and Coker 1992); and the microclimate (Stoutjesdijk and Barkman 1992). Lamprecht (1989) discerned three stories or vertical structures for tropical moist montane forests. The highest density of stems and number of species were found in the lower story. Senbata (2006) recorded an abundance of upper-canopy trees in the Bonga and Maji forests of southwestern Ethiopia. Even though only a few tree species are represented in the upper story, these trees are species with a regular distribution in all of the stories (Lamprecht 1989). The emergent trees in this layer were *Celtis africana* and *Poteria adolfi-friedericii*, each contributing 26.67% of the height in this stratum. About 60.8% of the total basal area involved five tree species in the upper story: *Celtis africana*, *Pouteria adolfi-friedericii, Acokanthera schimperi, Albizia schimperiana, and Millettia ferruginea.* Lamprecht (1989) noted that the highest dominance (basal area) values are found in the upper story, with a lower percentage in the middle story and the lowest percentage in the lower story. Förster 1973 (Lamprecht 1989) found percentages of 43%–48% in the upper story, 34%–40% in the middle story and 13%–23% in the lower story of a Colombian rainforest. In the present study, dominance values were 36.23% in the upper story, 41.66% in the middle story, and 22.06% in the lower story. Apparently, the lack of dominance value for the upper story in this study is due to selective logging of the upper story trees. In terms of density, the largest values are found in the lower strata compared to the middle and upper stories. In the present study, 75% of the tree density is concentrated in the lower strata.

Conclusions

The ongoing deforestation at Wondo Genet has thinned out the trees and significantly altered the vertical and horizontal structural characteristics. The overall forest diameter-class frequency distribution depicted the conventional inverted-J shaped curve that is typical of an expanding population distribution pattern with balanced recruitment and death. However, at the individual species level this pattern has changed with several species showing very low recruitment or discontinuous reproduction. The forest's overall basal area is also quite low. Because of the low density and low basal area, timber cutting, legal or illegal, should be avoided until the forest regains its capacity. Enrichment planting for species that have low densities or broken population structures is required. Assisted natural regeneration will also accelerate the recovery process. Most importantly, all silvicultural interventions should be preceded by reducing the anthropogenic disturbance, such as illegal logging and fuel wood collection. As a secondary forest, progress can made if disturbance factors, mainly anthropogenic, are reduced. Further studies should focus on determining the makeup of the historical forest prior to intensive cutting, an inventory of the forest plants, the needs of individual species for natural regeneration, and the annual growth for the various tree species. Ethnobotanical studies should be carried out since the surrounding communities rely on the medicinal values of the forest. Permanent plots should be established to monitor the forest growth dynamics. Soil and water related studies should be also

conducted. Since the carrying capacity of this remnant forest cannot sustain the demands of the increasing population surrounding the forest, stakeholders at all levels must be involved in designing and implementing solutions for the conservation of this resource.

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